EFFECTS OF WATER FLOW ON THE DETACHMENT OF SOME AQUATIC PULMONATE GASTROPODS

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ABSTRACT

Detachment behaviour of several taxa of aquatic pulmonate molluscs was studied in a tubed, flowing water system. The species investigated were *Lymnaea peregra* (Müller), *L. stagnalis* (L.), *Planorbis planorbis* (L.), *P. vortex* (L.), *Bulinus jousseaumei* (Dautzenberg), *Biomphalaria glabrata* (Say) and *Physa fontinalis* (L.). The discharge of water encountered by the snail before detachment was measured in relation to several factors, which included shell profile exposed to the current, body mass and foot area. Using analysis of variance and multiple regression techniques, profile was found to be the predictive variable for most of the species tested. There were negatively sloped linear relationships between profile and detachment time. Planispiral shaped snails such as *Biomphalaria* and *Planorbis* had the most direct relationships. The more globose snails such as *Bulinus* and *Lymnaea* had much less predictable responses. There were interspecific differences between snails in their detachment times, and for *L. peregra* at least, time of year and feeding regime were also important variables.

Aquatic gastropods can be vectors of a number of helminth infections including schistosomiasis and fascioliasis. The introduction of irrigation channels from areas in which there is a degree of infection into areas where there is little degree of infection can seriously increase infection rates in local host populations. For some time, engineers have been aware of these risks and have attempted to take these factors into account in channel design (Araoz, 1962). Research in which snails are exposed to different velocities of water flow in experimental channels has helped to determine many of the design criteria. For example, Jobin and Ippen (1964) investigated the behaviour of *Biomphalaria glabrata* (Say) in open channels. Firstly, empty shells, tethered to a Newton meter, were used to measure drag forces and secondly, measurements of absolute snail strength were made, thereby leading to the prediction that the snails would probably dislodge at a flow rate of 0.94 m·s⁻¹. When live snails were tested in flowing water, the prediction came close to being fulfilled, with snails dislodging at 0.65 m·s⁻¹.

Although Jobin and Ippen (1964) measured the maximum velocity at which snails could retain their grip, little measurable correlation was found between snail size and ability to stay attached. It was necessary to make sensible use of envelope curves to graphically represent the relationships between (a) water velocity at which detachment occurred and (b) the diameter of the ramshorn, or planispiral, shaped shells. A similar pattern of results for *Biomphalaria pfeifferi* (Krauss) was obtained by Madelin (1984) although detachment velocities were lower at 0.33 m·s⁻¹.

Experiments have also been done on other, non-vector species including *Stagnicola palustris* (Müller) and *Physa propinqua* (Tryon) (Moore, 1964). This research involved the use of snails in open channels but in a multivariate experimental design. The number of snails detaching at different velocities on a variety of substrata were measured, and it was possible to show a curvilinear relationship of detachment velocity with snail shell length; substratum type appeared to be a highly significant variable. Flow rates were measured with a mechanical, propellor driven, flow meter.

These works did not take particular account of the fatiguing effect of continuous exposure to a flow of water. Dorier and Vaillant (1948) did take this factor into account to a limited extent in their studies on a variety of invertebrate species including *Theodoxia fluviatilis* (L.), *Ankylastrum fluviatile* (Müller), *A. capuloides* (Jan.), *Radix limosa* (L.), *Physa fontinalis* (L.), *Bythinia tentaculata* (L.) and *Lymnaea stagnalis* (L.). A Pitot tube was used to measure local water velocity at depths as low as 3mm from the substratum. *R. limosa* and *L. stagnalis* detached at flow rates of 0.202 and 0.75 m·s⁻¹ respectively but snail structural dimensions were not taken into account.

The aims of the present work were therefore, (1) to devise an apparatus in which aspects of snail detachment behaviour could be investigated, (2) to identify dimensional aspects of snail hydrodynamics which might be related to detachment and (3) to compare the detachment performance of a range of species, including some schistosomiasis vectors. The species investigated were an albino and a pigmented

form of the schistosome vector *Biomphalaria glabrata; Bulinus jousseaumei* (Dautzenberg) which is also a schistosome vector; *Lymnaea peregra* (Müller) which can be a liverfluke vector; *Physa fontinalis* (L.), a snail commonly found in pond weed; *Lymnaea stagnalis* (L.), *Planorbis planorbis* (L.) and *P. vortex* (L.) which are all still-water snails. The first two species are tropical and the remainder are wild snails in the United Kingdom.

MATERIALS AND METHODS

The previously described experiments used square sectioned open channels. I used similar channels in preliminary trials but felt that the corners and broken water surface presented an unnecessarily complicating factor at this stage of the work. The effect of flow in a round sectioned tube was therefore investigated.

The apparatus design is given in figure 1. An Otter water pump with a maximum capacity of 0.5 dm·s^{-1} was used to deliver water to an upper reservoir of 15 dm^3 capacity, 0.57 m above a similar sized lower reservoir. Suitable overflows were used to maintain a constant head of water, which was delivered to the test chamber through a calibrated gate valve. The discharge rate at each valve opening was empirically obtained by measuring the time taken to discharge 10 dm^3 to an empty chamber; this converts to an average flow rate of 0.86 m·s^{-1} at maximum discharge.

The tubing and test chamber were made of transparent poly-vinyl chloride (PVC) tubing (internal diameter 0.025 m) connected by push fittings. Snails could be easily introduced to the test chamber by closing the gate valve, emptying the lower chamber and introducing the snail into the empty test chamber which had previously been wetted. The snails, which were tested singly, usually attached within 30 seconds. By lowering the upstream end of the test chamber, and by slowly opening the gate valve, snails could be fully immersed without encountering turbulence. The lower reservoir was then filled, the test chamber made horizontal and the pump started. The gate valve was opened one stop per 10 seconds, thereby exposing the snail to a known discharge.
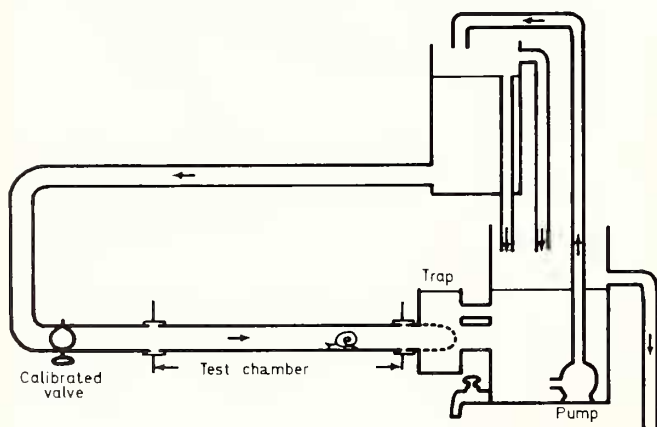

Fig. 1. Design of the apparatus.

At maximum velocity, the length of time until the snail detached was recorded. Since the discharge at maximum flow was known, the total discharge as m^3 · s encountered by the snail from the start of the experiment up to detachment could be calculated. Similarly, approximate velocities of flow in the pipe could be calculated, though this was not the prime intention. Data on velocity are, however, useful for comparison with results of other authors. A capillary bore manometer was used to measure the local relative flow rate at intervals of 2 mm from the wall of the tube to its centre.

A video camera system was used to visualise the flow in the test chamber. Black particles of Zeocarb, which has a slightly negative buoyancy, were fed into the system. Freeze frame photographs were taken of the video screen and it was possible to follow the paths of particles in tubes with and without snails present.

As well as the detachment time for each snail tested in the apparatus, a number of other parameters were measured. Mass was obtained by weighing a live snail from which excess water had been blotted. Area of the foot when fully extended was measured by allowing the snail to crawl on a plastic petri-dish. A stylus could then be used to scratch the outline of the foot from underneath. This outline was placed over a piece of mm graph paper and squares counted. The area of the smallest profile was obtained by placing the snail in the light path from a distant light source and tracing the outline of the shell on graph paper before counting squares. The area of the largest profile was obtained in a similar way, but this aspect was not found to be significant in the analysis and these data were ignored.

The absolute strengths of a number of snails were measured. Jobin and Ippen (1964) obtained their results by putting a small harness on the snail under investigation; they then used gramme masses to cause the snail to detach. It is difficult to treat such data as a continuous variable and I therefore allowed a snail to become mobile in water in a dish on the top of an Oertling top pan balance. The force that the snail exerted to maintain its grip while being gently lifted off was then measured. The balance gave an output to a chart recorder; this meant that the application of a firm continuous pull could be verified. Various mechanical devices including pulleys and harnesses were tried, but the most effective and reliable method of removing the snails was to first gently tease and then lift the snail by forceps.

RESULTS

Reynold's number (R) for a flowing water system is a dimensionless value that can indicate whether flow is smoothly laminar or turbulent (Cartwright, 1985). The number is given by

$$R = \frac{\varrho \, v \, d}{n}$$

where ϱ = density of liquid kg·m^{-3} (1000 for water), v = velocity m·s^{-1} (0.860 for this system), d = diameter of tube (0.025 m), and n = viscosity of water (0.0013 N·s·m^{-2}).

In natural waters, stream flow is almost always turbulent (Hynes, 1970). In my experiments, R = 16,538 at maximum velocity, which is just about the turbulent flow threshold value of R = within 1100-50,000. When the test chamber was empty of snails, the video recording showed a slight sinuous tracking of particles. When snails were present, turbulent eddies (Karman street vortices) were visible downstream of the snail (Fig. 2). Local flow rate measurements, obtained by use of a capillary manometer showed a velocity profile transitional between those characteristic of laminar and turbulent flow (Fig. 3).

The drag coefficient (cd) for a snail is given by the equation

$$cd = \frac{2f}{a \cdot \varrho \cdot v^2}$$

where f = resistive force, a = area exposed to the flow, ϱ = density of water, v = velocity of water.

Joppen and Ippen (1964) measured resistive force by empirical determinations on tethered shells. Unfortunately, since my experiments were conducted in a closed tube, it was not possible to use a similar technique. However, Stokes' law states (Collieu and Powney, 1977) that the resistive force of a spherical body (f) in a uniform velocity field is given by the equation

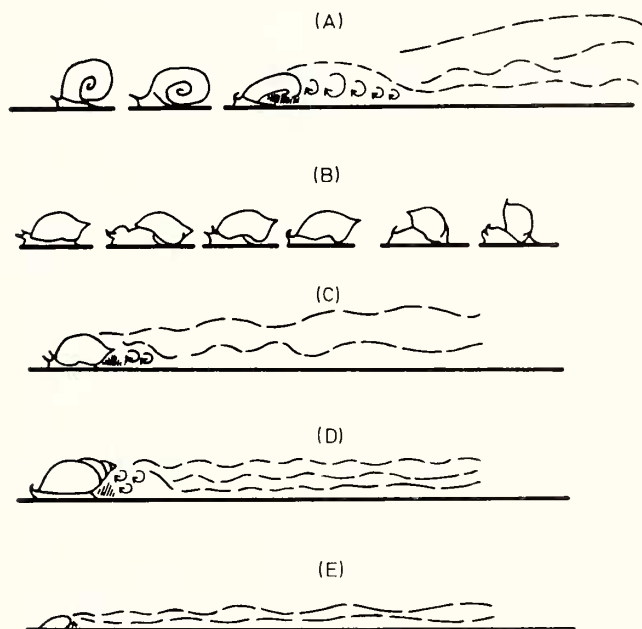$$f = 6 \pi \cdot \eta \cdot r \cdot v$$

(A)

(B)

(C)

(D)

(E)

Fig. 2. Behaviour, stream lines and vortices downstream of the snails. (A) Planospiral snail changing shell position as flow increases. The last diagram shows the stream lines and vortices at maximum flow. (B) Characteristic movement of *Lymnaea peregra* as flow increases. The last diagram shows the shell position immediately before detachment. (C) Stream lines and vortices for *L. peregra*. (D) Stream lines and vortices for *L. stagnalis*. (E) Stream lines and vortices for *Bulinus jousseaumei*.
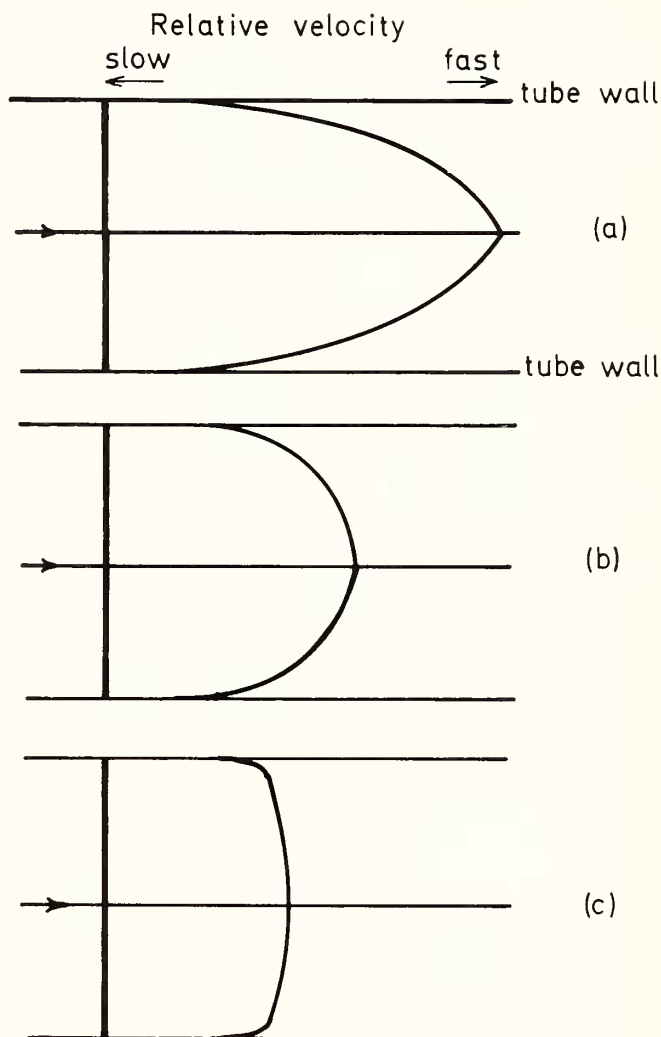

Fig. 3. Velocity profiles for (a) smooth flow, (b) transitional flow and (c) turbulent flow (after Duderstadt *et al.*, 1982).

where η = viscosity, r = radius of sphere, and v = velocity of flow.

On a snail of approximately spherical shape such as *Lymnaea peregra* and diameter of 0.006 m, f = 6.3 x 10^{-5} N. Stokes' law only applies in smooth flow and the flow here might have been just turbulent enough to negate the valid application of the law. Stokes' law also presumes that the object is free of any nearby surfaces, which is not the case here since the mollusc is attached. The drag coefficient for a typical specimen of *L. peregra* was thus calculated to be 0.0053 which compares with a value of approximately 0.6 obtained by Jobin and Ippen (1964) for *Biomphalaria glabrata*. The discrepancy is almost certainly due to the limited applicability of Stokes' law and indicates that resistive force should be measured using methods similar to those of Jobin and Ippen.

Many of the previous authors have described consistently similar patterns of behavior. For example, snails

would initially move randomly, next orientate with their heads upstream and then make regular movements to pull the shell over the foot, before finally detaching. In addition to confirming these general patterns of behavior, I observed some interspecific differences. For example, the planospiral taxa (*Biomphalaria* and *Planorbis*) would initially hold the shell erect whilst facing upstream so that the shell acted like a rudder. As velocity increased, the shell would be held at an increasingly acute angle to the substratum. At higher velocities, the shell would be held parallel with and close to the substratum, in the zone of slowest water flow. The columella muscle and associated viscera would be stretched several millimetres from shell to foot mass before the snail eventually detached. Globose molluscs (*Lymnaea*) would follow the general pattern for molluscs described previously by other authors such as Jobin and Ippen (1964). In addition, after some time at high velocities, snails would first lose control of the columella muscle so that the shell would be swept downstream of the foot and would then yaw violently, with the snail periodically trying to gain control and achieving this for short periods. Eventually the part of the shell normally held over the head would lift up into the zone of fastest moving water and the snail would immediately detach. By contrast, *B. jousseaumei* clamped down, did not lose control in stages and eventually detached instantaneously. *B. jousseaumei* had a shell shape superficially similar to *L. peregra* but the shell was more glossy with a smoother profile. Data from all species tested were used to attempt to find a relationship between parameters of size and flow encountered at maximum velocity. Data were $\log_{10}$ transformed, to normalise each variable and ensure the validity of parametric statistical analysis. In almost all cases, transformation improved the significance of relationships. Multiple regression analysis of flow as $dm^3 \cdot s$ before detachment (Y) in relation to mass (X_1), foot size (X_2) and profile (X_3) of all snails gave the following equation:

$$Y = 2.42 + 0.0874X_1 + 0.242X_2 - 0.748X_3$$

(t values of 0.54 for X_1, 1.83 for X_2 and -3.35 for X_3; $F_{3,409}$ = 16.7 P <0.001).

Detachment flow as $dm^3 \cdot s$ was plotted against the most significant variable from the multiple regression for the data from all the species, in order to partially visualise the relationship uncovered by the mulitple regression (Fig. 4). The data showed a considerable amount of scatter, suggesting that some stochastic term needs to be included in future analyses. Nevertheless, there was a highly significant negative linear slope ($F_{1,412}$ = P <0.001) which suggested that snails with larger profiles would detach at lower flows. Further analyses therefore concentrated on the profile rather than mass or foot size.

It might be thought that the relationship between profile size and flow described above was predictable and hardly worthy of comment. However, the relationship was not always so obvious when data for individual species were selected from the data matrix and detachment flow was plotted against profile. Some taxa failed to show a relationship, probably through lack of data (e.g. *Physa fontinalis, Biomphalaria*
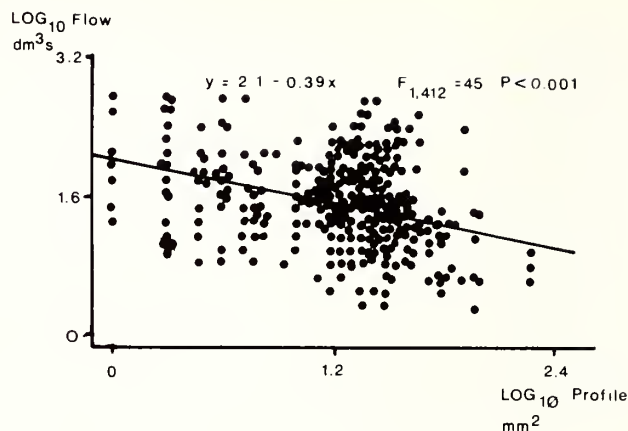

Fig. 4. Relationship between detachment flow and profile area for all snails used in these experiments.

jousseaumei and *P. vortex*). For the taxa which showed significant linear or multiple regression relationships, data were plotted in figures 5-9. A pigmented population and an albino population of *B. glabrata* were included in order to identify intraspecific variation. The planospiral snails (Figs. 5-7) showed a more obviously linear relationship than the more globose snails (Figs. 8-9).

Attempts were made to obtain a size index which would relate more closely to detachment flow than profile alone. The following relationship was used:

size = (foot size/profile) x mass.

This index gave significant regression relationships for several species, sometimes improving on the F values obtained in the regressions where profile alone had been used as the independent variable. For example, for *Planorbis planorbis* the new value was F = 6.9 compared with F = 5.2.

Of the species studied here, *Lymnaea peregra* is the most likely to encounter flowing water and so more attention was focussed on this snail. A multiple regression analysis of detachment flow on mass, foot size and profile gave a significant relationship ($F_{3,168}$ = 4.2, P<0.01). The regression equation is given in Table 1. No investigation of the allometric relationships between foot size, profile and mass were made, since this was not the main subject of the present study, though results of such an investigation might slightly improve the performance of the index described above by introducing a cubic power function for body mass and squared functions for foot area and profile.

Studies on *Lymnaea peregra* took place over a period of approximately 6 months, during which time snails were kept in the laboratory, and fed on boiled dried lettuce. Some snails deposited eggs during their natural egg laying period in early spring. A one-way analysis of variance was carried out on detachment flow, with time of year as the factor under investigation. A significant effect of time was found (Table 2), which could be due to the diversion of metabolic resources to egg laying during the period of study. However, data for *Biomphalaria glabrata* and *Planorbis planorbis* were available in which individual snails had been tested before and after
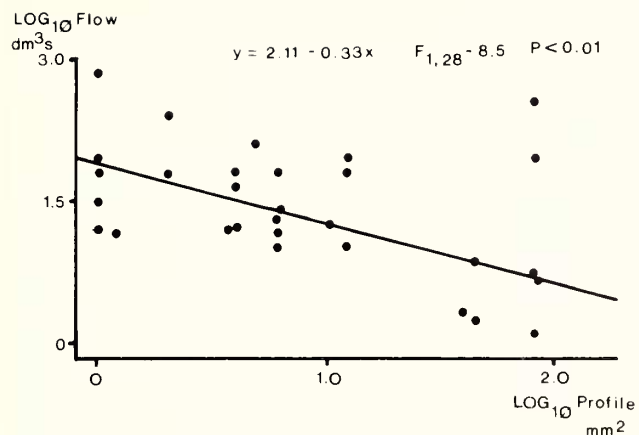
$$y = 2.11 - 0.33x \quad F_{1,28} - 8.5 \quad P < 0.01$$

Fig. 5. Relationship between detachment flow and profile area for *Biomphalaria glabrata* (pigmented).

$$y = 2.21 - 0.57x \quad F_{1,63} - 19.6 \quad P < 0.001$$
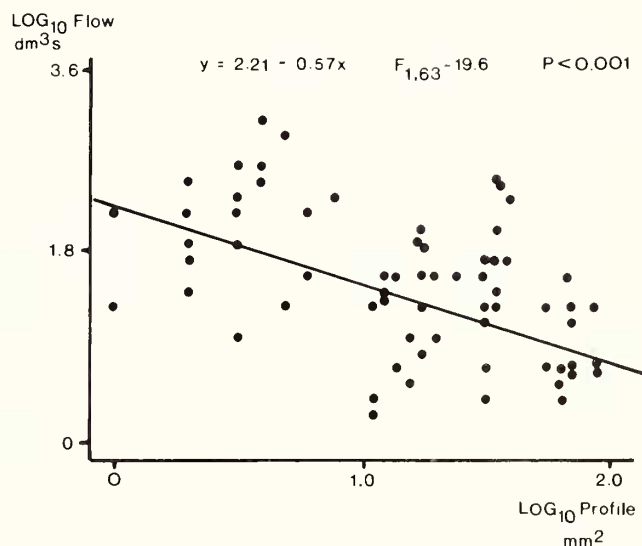
Fig. 6. Relationship between detachment flow and profile area for *Biomphalaria glabrata* (albino).

$$y = 2.8 - 0.89x \quad F_{1,34} - 53 \quad P < 0.01$$
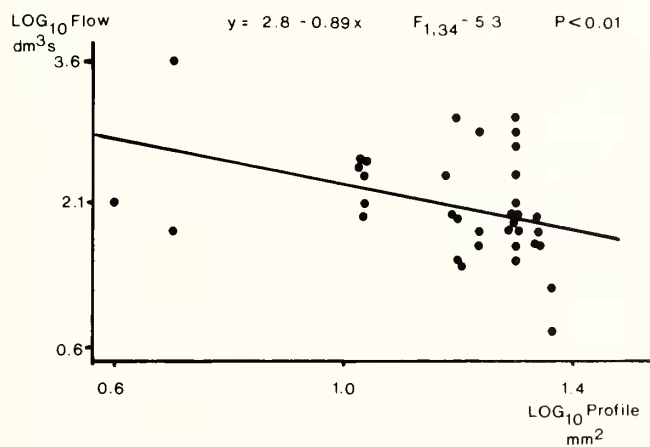
Fig. 7. Relationship between detachment flow and profile area for *Planorbis planorbis*.

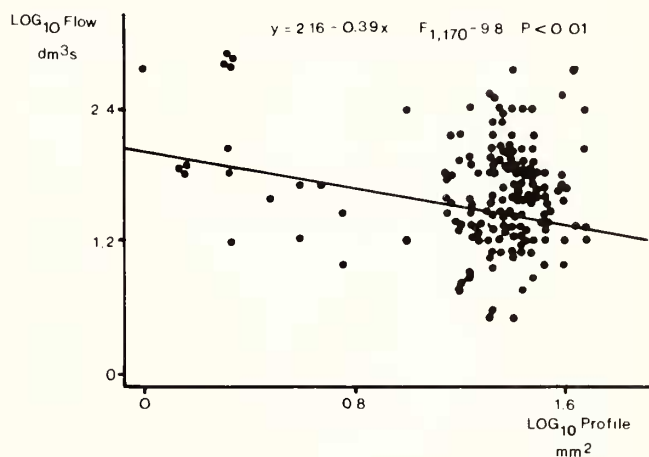$$y = 2.16 - 0.39x \quad F_{1,170} - 9.8 \quad P < 0.01$$

Fig. 8. Relationship between detachment flow and profile area for *Lymnaea peregra.*
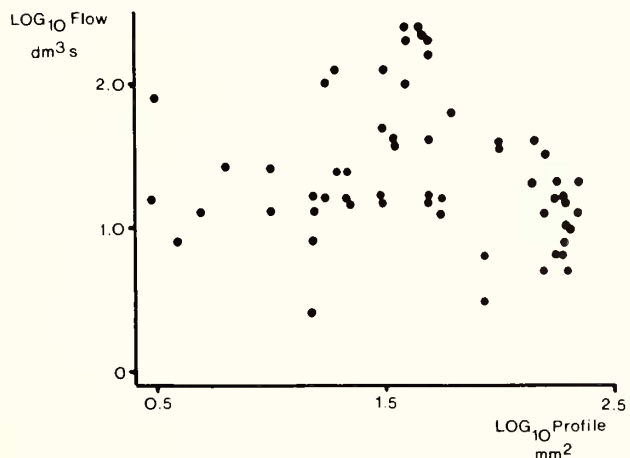
Fig. 9. Plot of detachment flow against profile for *Lymnaea stagnalis.*

egg laying. No statistically significant effects on detachment were noted but the data set was small and the experiment could be usefully repeated for these and other species.

Effects of substratum type were investigated by inserting a piece of coarse carborundum paper firmly into the test chamber. This had no measurable effect on the discharge through the pipe. No significant difference in detachment flow was noted between populations of *Lymnaea peregra* which were on the rough surface or the smooth surface of the PVC tube.

Effects of feeding were investigated by maintaining a population of *Lynmaea peregra* for one week without food prior to testing. Analysis of variance showed that food was a significant factor (Table 2). However, it was surprising to note that fed snails detached at lower velocities than unfed snails.

Table 1. Results of multiple regression analyses for detachment flow ($dm^3 \cdot s$) in relation to mass (x_1), foot size (x_2) and profile (x_3). Only snails showing significant relationships are included. All data were $\log_{10}$ transformed.

	Intercept	x_1	x_2	x_3			
All species							
Coeff.	2.42	+0.087	+0.242	—0.75	$F_{3,409}$ =	16.7	P <0.001
St. dev.	0.45	0.16	0.13	0.22			
Lymnaea peregra							
Coeff.	1.37	—0.296	+0.70	—0.66	$F_{3,168}$ =	4.2	P <0.01
St. dev.	1.14	0.41	0.43	0.54			
L. stagnalis							
Coeff.	7.66	+2.36	—0.24	—0.32	$F_{3,53}$ =	3.5	P <0.05
St. dev.	2.1	0.83	0.33	1.15			
Planorbis planorbis							
Coeff.	2.82	—0.036	+1.19	—1.83	$F_{3,31}$ =	2.9	P = 0.05
St. dev.	1.52	0.58	1.11	0.68			
Biomphalaria glabrata (albino)							
Coeff.	1.18	—0.339	—0.043	—0.024	$F_{3,61}$ =	6.7	P <0.001
St. dev.	1.28	0.43	0.29	0.69			
B. glabrata (pigmented)							
Coeff.	—2.19	—1.90	+2.09	+0.539	$F_{3,26}$ =	5.7	P <0.01
St. dev.	2.13	0.80	0.86	0.84			

Effects of temperature change were investigated by keeping *Lymnaea peregra* at 4°C for several days before testing them in the apparatus at a temperature of 22°C. Analysis of variance again showed a significant effect of this factor (Table 2). Snails which had not experienced a temperature change detached at an earlier time than cold adapted snails. This experiment might have been confounded with the previous one however; although fed and unfed snails were kept at low temperature before testing, the metabolism of the snails had slowed down to such an extent that snails which did have food did not consume it. Initial analysis of the data for *L. peregra* did not find any significant relationships between detachment flow and any aspect of size. In the light of the above experiments however, data relating to the temperature and food experiments were omitted and significant relationships then appeared in the regressions.

An analysis of variance was undertaken to compare mean detachment time for all taxa investigated here. Results are given in figure 10. Although there was a highly significant variation between taxa ($F_{6,379}$ = 7.4, P<0.001) there was no obvious pattern in the relative means. Table 3 shows the maximum velocities endured for at least one minute by snails in my experiments by comparison with other authors. It is difficult to compare results with other authors since snail sizes are not always given. For the sake of the comparison, I assumed that mature snails had been used.

In the lifting experiments on *Lymnaea peregra* preliminary investigations showed that approximately 50 trials over 30 minutes were needed before a full sized specimen of *L. peregra* began to show fatigue. Means of 15 trials were therefore obtained but there was no relationship between size and strength. There did appear to be a possible relationship between absolute strength of *L. peregra* and it's ability to resist a flow for long periods but the relationship was not statistically significant ($F_{1,25}$ = 3.3, P <0.10). A similar in-

Table 2. Results of analyses of variance on several aspects of the biology of *Lymnaea peregra* in relation to detachment flow.

Factor	df	F	Significance
Time	1,179	4.7	P <0.001
Surface	1,195	1.9	
Food	1,195	7.1	P <0.01
Temperature	1,195	8.3	P <0.01

vestigation of *Planorbis planorbis* did not suggest any possible relationship. The globose *L. peregra* at an average mass of 0.273 g was able to exert an average force of 0.0385 N, approximately equivalent to 14 times it's own body mass in a vertical lift. By contrast *P. planorbis* at an average mass of 0.17 g exerted an average force of 0.019 N, approximately 11 times its' own body mass.

DISCUSSION

Studies similar to those described here have usually employed inclined flumes, with precautions taken to minimise turbulence in the channel; the velocity of the water was changed and the number of snails detaching at each velocity was recorded. Such a design makes results difficult to interpret if snails can stay attached at the highest velocity provided. Also, snails can interact with the surface and the corners in box sectioned channels. In biological terms, the tube is much more controllable, though the physics of flow in tubes is complicated. The video camera proved to be a useful device for examining the effect of mollusc on the flow pattern in the tube. Vortices could be seen and it was noticeable that certain species such as *Lymnaea stagnalis* appeared to produce a non-expanding vortex pattern, whilst others such
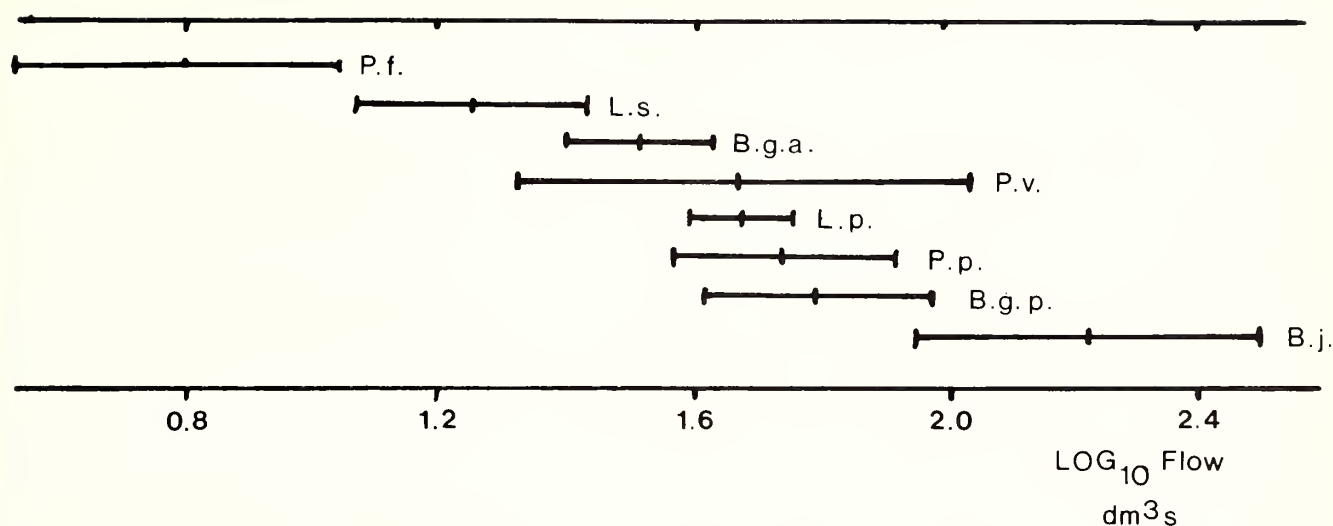
Fig. 10. Comparison of mean detachment flow for each species, together with 95% confidence intervals. An analysis of variance showed significant variation between species (P < 0.001). P.f. = *Physa fontinalis*; L.s. = *Lymnaea stagnalis*; B.g.a. = *Biomphalaria glabrata* (albino); P.v. = *Planorbis vortex*; L.p. = *L. peregra*; P.p. = *P. planorbis*; B.g.p. = *B. glabrata* (pigmented); B.j. = *Bulinus jousseaumei*.

Table 3. Comparison of maximum velocities endured by a variety of species investigated here and in other published work. It was presumed that results were based on performances of adult snails.

Dorier and Vaillant	*Theodoxia fluviatilis*	2.4 m·s⁻¹
(1964)	*Ancylastrum fluviatile*	2.4 m·s⁻¹
	A. capuloides	0.65 m·s⁻¹
	Radix limosa	2.02 m·s⁻¹
	Physa fontinalis	0.89 m·s⁻¹
	Bithynia tentaculata	0.82 m·s⁻¹
	Lymnaea stagnalis	0.75 m·s⁻¹
Jobin and Ippen (1964)	*Biomphalaria glabrata*	0.65 m·s⁻¹
Moore (1964)	*P. propinqua*	0.84 m·s⁻¹
	Stagnicola palustris	0.80 m·s⁻¹
Madelin (1984)	*B. glabrata*	0.33 m·s⁻¹
Dussart (1985)	*B. glabrata*	0.86 m·s⁻¹
	L. peregra	0.86 m·s⁻¹
	L. stagnalis	0.70 m·s⁻¹
	Planorbis vortex	0.86 m·s⁻¹
	P. planorbis	0.86 m·s⁻¹
	Bulinus jousseaumei	0.86 m·s⁻¹
	P. fontinalis	0.66 m·s⁻¹

as *Biomphalaria glabrata* showed an expanding vortex pattern. The use of video techniques could allow much more sophisticated analyses to be made in the future.

The drag coefficient calculated for *Lymnaea peregra* was considerably different from the value for *Biomphalaria glabrata* obtained by Jobin and Ippen (1964). Even without invoking the inapplicability of Stokes law, some differences were expected since they used an equivalent to the large profile (diameter of the snail shell) rather than the area exposed to the current. They did justify the use of this dimension since they demonstrated that their snails did not perform significantly differently from standard spheres of similar size.

Regressions of detachment flow on size showed significant relationships when there were enough data. These relationships were more obvious for planispiral snails (Figs. 5-7) than for the others (Figs. 8-9). The small profile presented to water flow was the most significant predictor for detachment time. Relationships seemed to be linear with negative slopes such that larger snails detached earlier than smaller ones. This could be because larger snails are exposed to higher velocities as their shells protrude into faster flowing water. Alternatively, larger snails may be older and therefore more frail. If the latter were true however, a relationship between size and innate strength as shown by the lifting experiments might have been expected. No such relationship seemed to exist for *Lymnaea peregra*, though there was a possible relationship between strength and the ability to resist flow. There was absolutely no relationship between these factors for *Planorbis planorbis*.

There were significant differences between curves of the flow/profile regressions for the two *Biomphalaria* species (Figs. 5-6). Of species showing significant relationships, *Planorbis planorbis* had the highest slope (-0.89, Fig. 7) and *B. glabrata* (pigmented) had the lowest (-0.33, Fig. 5). Although no significant relationship could be shown for *B. jousseaumei*, this species withstood high flows for much longer than other snails. This was obvious in the analysis of variance, which compared the mean detachment times of all taxa.

Multiple regression equations reflected the results of the linear regressions; they showed that mass and profile were usually related to detachment flow through a negative slope, whereas foot area was usually related through a positive slope.

In some cases, closer relationships were obtained by using a size index, in which the foot area/ profile relationship was modified by the mass of the snail. With a smaller profile, or a bigger foot, the snail would be able to adhere for longer. The mass variable might operate through muscle

volume, enhancing attachment.

There was only a tenuous relationship between the size of *Lymnea peregra* and the flow at which it detached. It is worth noting that the planispiral species tested here are usually found in still waters, whereas *L. peregra* is found in both still and flowing waters. Most snails in flowing water would find themselves on rocks or vegetation, and therefore be able to move into local areas of low flow as necessary. Ambuhl (1962) convincingly demonstrated the existence of such zones behind boulders and Dorier and Vaillant (1954) showed that current speed could fall from 33 m·s⁻¹ in the main channel to less than 10 m·s⁻¹ in the centre of a *Potamogeton* stand. Nevertheless, a river snail might occasionally be exposed to high flow rates before it could find shelter, and it might therefore need some capacity to resist flow. The planispiral snails tested here may not be adapted to flowing conditions and may detach in a way which directly relates to their morphology. By contrast, *L. peregra* appeared to be better adapted to resisting detachment up to a certain limit of flow (1200 s at maximum flow rate), irrespective of size. The globose nature of the shell of *L. peregra* might confer a low drag coefficient such that physiological state, and proportion of smooth muscle in the columella muscle and foot muscle might be more important factors of detachment than size. Dorier and Vaillant (1954) classified the species they investigated into two groups; firstly 'rheobionts' including *Theodoxia fluviatilis* and *Ancylastrum capuloides* which could colonise exposed areas of moss and rock exposed to fast flows; secondly 'rheophiles' including *Radix limosa* which, although found in slower flowing conditions possessed ''a strong margin of security upon which they can call in exceptional circumstances, notably spates''. This observation is certainly confirmed in the present study.

More research could be done to investigate the relative importance of shape rather than size. Hughes (1979) notes that for objects in very low flows (creeping flow), streamlining may increase drag forces on the snail; at higher speeds, streamlining helps because it reduces drag by preventing the separation of flow lines downstream of the shell; conversely at high flows, surface protrusions can act as spoilers which reduce the wake and therefore reduce the drag. Such structural modifications of the shell may partly explain why the North American species *Io fluvialis* (Say) has a smooth outline in headwaters but is spinose in large rivers. Predation will of course be an important factor in governing the roughness of a shell. Interaction of predation and drag factors may explain why spinose and smooth shelled taxa can exist in the same riverine habitat. Flow characteristics of the environment can cause topological rather than structural modification of shell shape. ''Fluviatile species are also influenced greatly by the circumstances of their environment, those individuals inhabiting rough or disturbed waters, rapid and turbulent streams often show a shorter spire and a more expanded and larger mouth which necessarily allows for greater clinging or adhesive power and renders the mollusk less liable to be detached and probably injured by wave violence'' (Taylor, 1894).

Lymnaea peregra detachment did appear to be related to food availability and time of year. There was no pattern in the temporal relationship however, though egg laying might have been a significant factor. Contrary to the results of Moore (1964), the surface was not found to be a significant variable though the surface provided here was highly artificial.

In conclusion it appears that predictable relationships can be determined for many of the freshwater molluscan species investigated here, though the scatters are large and sufficient trials must be undertaken. Once such relationships are well understood, this experimental design could be used to investigate the hydrodynamics of shells. More practically, the influence of molluscicides on snail detachment could be investigated, as well as the possibility of pulsed flows leading to the accumulation of snails in distinct parts of the system. For example, once further basic information has been obtained, snail trapping weirs could be tested both in the laboratory and in the field, in association with molluscicide application.

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